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Faunal Exchanges between Siberia and North America

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With one Table

1. Introduction

I wish to announce a new dating technique that, for times subsequent to the refilling of the Mediterranean Sea 5.3 million years ago, has a minimum resolution of at least ±0.25 million years. In addition, it has direct climatic significance and can be correlated with other chronologies and biochronologies. It has a most specific bearing on faunal exchanges between Siberia and North America. It is called Vertebrate Paleontology.

More particularly, I speak of the vertebrate paleontology of the microtine rodents, the meadow mice, muskrats, lemmings, and relatives. They are hypsodont cricetid rodents with triangularly prismatic cusps on their teeth, and they probably include four discrete lineages having separate origins out of other cricetids. They are commonly grouped together taxonomically because of the similarity of their specializations. Their center of evolution was in Asia but possibly not their origins.

In the last 5 million years, the microtines have dispersed to every major landmass in the northern hemisphere, from the Arctic Ocean to the subtropics, from sea level to more than 16,000 feet in elevation, and from desert to swamp and lake. They live under the ground, on the ground, above the ground, and in the water. Their lineages usually reflect their particular ecologic preferences, although these preferences also change with time.

For the purpose of correlation, the particular values of the microtine rodents are their great and recent diversity, their ecologic selectivity, and their Asiatic center of diversity. When climatic changes have produced extensions of favorable environments, the microtines have dispersed, seemingly instantaneously, both eastward and westward out of Asia. From the records of Siberia (summarized by Vangengeim 1977), this is more logically envisioned as a southward dispersal out of northern Asia and adjacent Beringia into Europe, southern Asia, and North America.

The most useful test in constructing the North American biochronology of the microtine rodents has been the recognition of contemporaneous invasions in Europe. Available dates of microtine history in both continents have been mutually supporting and reinforcing. Thus, the microtine biochronology of Europe, which has developed over the past 15 years, has been greatly strengthened and improved by the development of the microtine biochronology of North America.

Supportive of this history, although not reinforcing because of the general absence of immigration waves, is the fossil record of microtine rodents in Siberia (Vangengeim 1977). This record indicates that, of the holarctic genera of microtine rodents known from the fossil record of Siberia, over 50% have their most ancient records in Siberia. In addition about 33% of these holarctic genera appear to have become extinct in Siberia at the time of, or some time after, their earliest appearance in Europe and North America. Presumably an undiscovered fossil history similar to that in Europe and North America will some day characterize southern Asia where many ancient forms now persist as relics in the living fauna. Similar relict faunas, fossil and living, are recognizable in Mexico and Central America (Burt 1949; Repenning & Ferrusquia, in preparation).

Ubiquitous as they are in the living fauna, the fossil remains of the microtine rodents are not found everywhere. Even where their fossils are present, eyes such as mine must

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get within three feet of the ground to see them. Because of the difficulty in finding fossil microtines, the U.S. Geological Survey, at the time of this writing, is two years into a project of collecting more abundant types of fossils, specifically freshwater diatoms and ostracodes, from microtine fossil localities. This is being done in hope that the remarkably precise microtine chronology can be used in defining and calibrating the biochronology of these more easily found invertebrates. The work is made more difficult by, but its success will be all the more useful because of, the extreme ecologic sensitivity of ostracodes and diatoms.

Dates based upon K-Ar years have been slightly altered to conform to the new decay and abundance constants recommended for adoption in August, 1977, by the IUGS Subcommission on Geochronology (see MANKINEN & DALRYMPLE 1979).

2. Barriers

In general terms, the barriers against dispersal of the microtine rodents to Europe and to North America seem to have been similar; high sea levels produced a Bering Strait and they also flooded the Arctic lowlands southward toward the Ural Mountains and apparently the Caspian lowlands northward toward the Ural Mountains; the southern limit of the Caspian Sea is south of the range of nearly all microtine rodents.

However, waves of microtine dispersal occurred before the frequent fluctuations of sea level that characterize the Pleistocene. These rodents are fundamentally grassland animals; climatic conditions that would have placed forested barriers around Beringia would also have extended forests northward along the Ural Mountains to the Arctic Ocean. Much remains to be determined, however, regarding the details of dispersal inhibitors. In fact, until the history of the microtine rodents in Asia is better known, the history of microtine dispersal throughout Holarctica will be incomplete. Nevertheless, at present the pattern of dispersal seems very convincing.

Other barriers to microtine dispersal exist. These rodents are arctic to temperate animals; only a few have entered the subtropics, yet some now live as far south as Guatemala, northern Burma, northern India, and Israel. Most of these now live at high elevations surrounded by tropical lowlands and are stranded in these locations by the disintegration of formerly more extensive temperate climates. In such situations are found many "living fossil" microtines (REPENNING & FERRUSQUIA, in preparation).

Although many microtines are well adapted to arctic conditions, extensive ice is also a barrier, and provincialism in fossil faunas of temperate North America clearly demonstrates the development of two dispersal avenues from Beringia on either side of the Cordilleran ice field and thus dates the beginning of the Ice-Free Corridor.

3. Correlation of Dispersals

The first lemming known in western Europe is found in association with one of the first records of the well-known *Elephas-Leptobos-Equus* fauna of Europe, for many years considered to signal the beginning of Villafranchian time. The oldest date in Europe associated with this fauna is between 3.5 and 3.6 m.y. ago (Les Etouaires, SAVAGE & CURTIS 1970); the immigration could be somewhat older but is definitely younger than a fauna correlated with that in the type section of the Villafranchian and dated as about 3.9 m.y. old (Vialette, SAVAGE & CURTIS 1970).

The oldest dated fauna marking the correlative invasion in North America is found in a vertical succession of mammalian faunas near Hagerman, Idaho, and lies stratigraphically below a bed dated at 3.5 m.y. and above beds recording the Cochiti normal polarity event, according to NEVILLE a. o. (1979). This event has been dated as ending about 3.8 m.y. ago. Interpolation based upon stratigraphic thickness suggests an age of about 3.7 m.y. for this invasion of North America and, as such, narrows the uncertainty of the age of the European invasion. That is, it does so under the hypothesis of synchronous holarctic dispersal events of the microtine rodents.

In this example, as well as all others, there is no possible confusion of dispersal events for, in this example, in both Europe and North America the preceding dispersal was a full 1 m.y. earlier and the next was more than 1 m.y. later. Dates in both continents eliminate the possibility of misidentifying a dispersal event.

In many holarctic dispersal events the types of microtine rodents that entered Europe were not those that entered North America. With respect to the dispersal event 3.7 m.y. ago, the lemming genus *Synaptomys*, and at least one other microtine that is unknown in North America, entered western Europe; the first muskrat *(Pliopotamys)* was the North American immigrant of this dispersal event and this microtine is unknown in Europe. In this case, and others, there is little basis for correlation by similarity of microtine immigrants.

One m.y. earlier, at 4.8 m.y., two forms appear abruptly in both Europe and North America and they are part of well-known lineages; it is possible to say that they appear at similar stages of evolution. More than 1 m.y. later, at 2.6 m.y., two subgenera of one genus of lemming [*Synaptomys (Synaptomys)* and *S. (Mictomys)*] first appear in North America; one subgenus [*S. (Synaptomys)*] had appeared earlier in Europe, but the other is never known in Europe. The lemming genus *Lemmus* appeared at this time in Europe but did not appear in North America until the late Pleistocene.

Thus, although the older recognized holarctic microtine dispersal events show similar forms emigrating to both Europe and North America, later ones, beginning with that which introduced muskrats to the North American fauna, differ to some degree in composition. In addition a genus may appear in different continents during different dispersal events.

The differences in immigrants during particular microtine dispersal events appear to relate to the development of provincialism in the Siberian microtine fauna. From the Ural Mountains to the Bering Strait, Siberia, extends some 160° of longitude, nearly half way around the Holarctic World, and, beginning at least 3.7 m.y. ago, there appear to have been provincial differences in the microtine faunas at either end, at least, of Siberia.

In the last 5.3 m.y. there are at least 10 recognizable microtine faunas in North America. A similar number are recognizable in Europe. Eight of these are recognizable by the abrupt and usually abundant appearance of exotic microtines in the endemic faunas. The remaining two are recognizable by significant endemic evolution in both North American and European faunas but cannot be correlated between continents. These endemic faunas evolved during the two longest periods of no intercontinental faunal dispersal: between 4.8 and 3.7 m.y. ago and between 3.7 and 2.6 m.y. ago.

During the second of these prolonged periods of no dispersal the first Beringian transgression of HOPKINS (1967) took place and the first North Pacific mollusks dispersed to Iceland at about 3 m.y. ago, according to GLADENKOV (1976). The conclusion of this time of no dispersal was marked by the appearance of the first lemmings in the North American fauna about 2.6 m.y. ago and correlates very well with North Pacific deep sea records that indicate pronounced cooling and the first major glacial episode in the Arctic region (SHACKLETON & OPDYKE, 1977). This first major glacial, although pronounced in the marine record, is judged by SHACKLETON & OPDYKE to have been only about two-thirds as intense as late Pleistocene glacial epochs on the basis of oxygen isotope composition. Nevertheless, BOELLSTORFF (1978) has recently called attention to a pre-Nebraskan till of this approximate age at Afton, Iowa.

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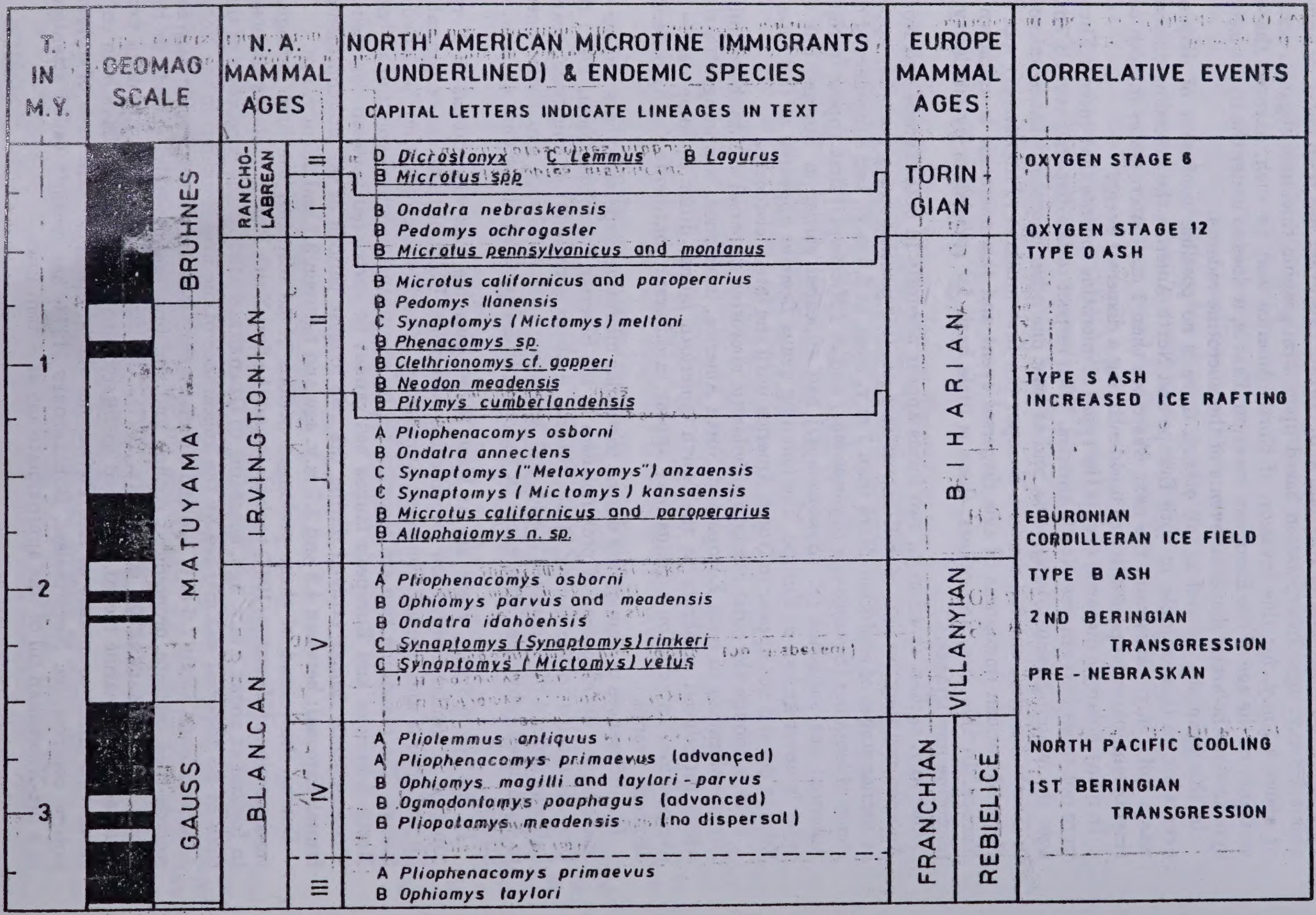

T. IN M.Y.	GEOMAG SCALE	N.A. MAMMAL AGES		NORTH AMERICAN MICROTINE IMMIGRANTS (UNDERLINED) & ENDEMIC SPECIES CAPITAL LETTERS INDICATE LINEAGES IN TEXT	EUROPE MAMMAL AGES	CORRELATIVE EVENTS
	BRUHNES	RANCHOLABREAN	II	D Dicrostonyx C Lemmus B Lagurus B Microtus spp	TORINGIAN	OXYGEN STAGE 6
			I	B Ondatra nebraskensis B Pedomys ochrogaster B Microtus pennsylvanicus and montanus		OXYGEN STAGE 12 TYPE O ASH
1	MATUYAMA	IRVINGTONIAN	II	B Microtus californicus and paroperarius B Pedomys llanensis C Synaptomys (Mictomys) meltoni B Phenacomys sp. B Clethrionomys cf. gapperi B Neodon meadensis B Pitymys cumberlandensis	BIHARIAN	TYPE S ASH INCREASED ICE RAFTING
			I	A Pliophenacomys osborni B Ondatra annectens C Synaptomys ("Metaxyomys") anzaensis C Synaptomys (Mictomys) kansaensis B Microtus californicus and paroperarius B Allophaiomys n. sp.		EBURONIAN CORDILLERAN ICE FIELD
2		BLANCAN	V	A Pliophenacomys osborni B Ophiomys parvus and meadensis B Ondatra idahoensis C Synaptomys (Synaptomys) rinkeri C Synaptomys (Mictomys) vetus	VILLANYIAN	TYPE B ASH 2ND BERINGIAN TRANSGRESSION PRE - NEBRASKAN
3	GAUSS		IV	A Pliolemmus antiquus A Pliophenacomys primaevus (advanced) B Ophiomys magilli and taylori - parvus B Ogmodontomys poaphagus (advanced) B Pliopotamys meadensis (no dispersal)	FRANCHIAN / REBIELICE	NORTH PACIFIC COOLING 1ST BERINGIAN TRANSGRESSION
			III	A Pliophenacomys primaevus B Ophiomys taylori		

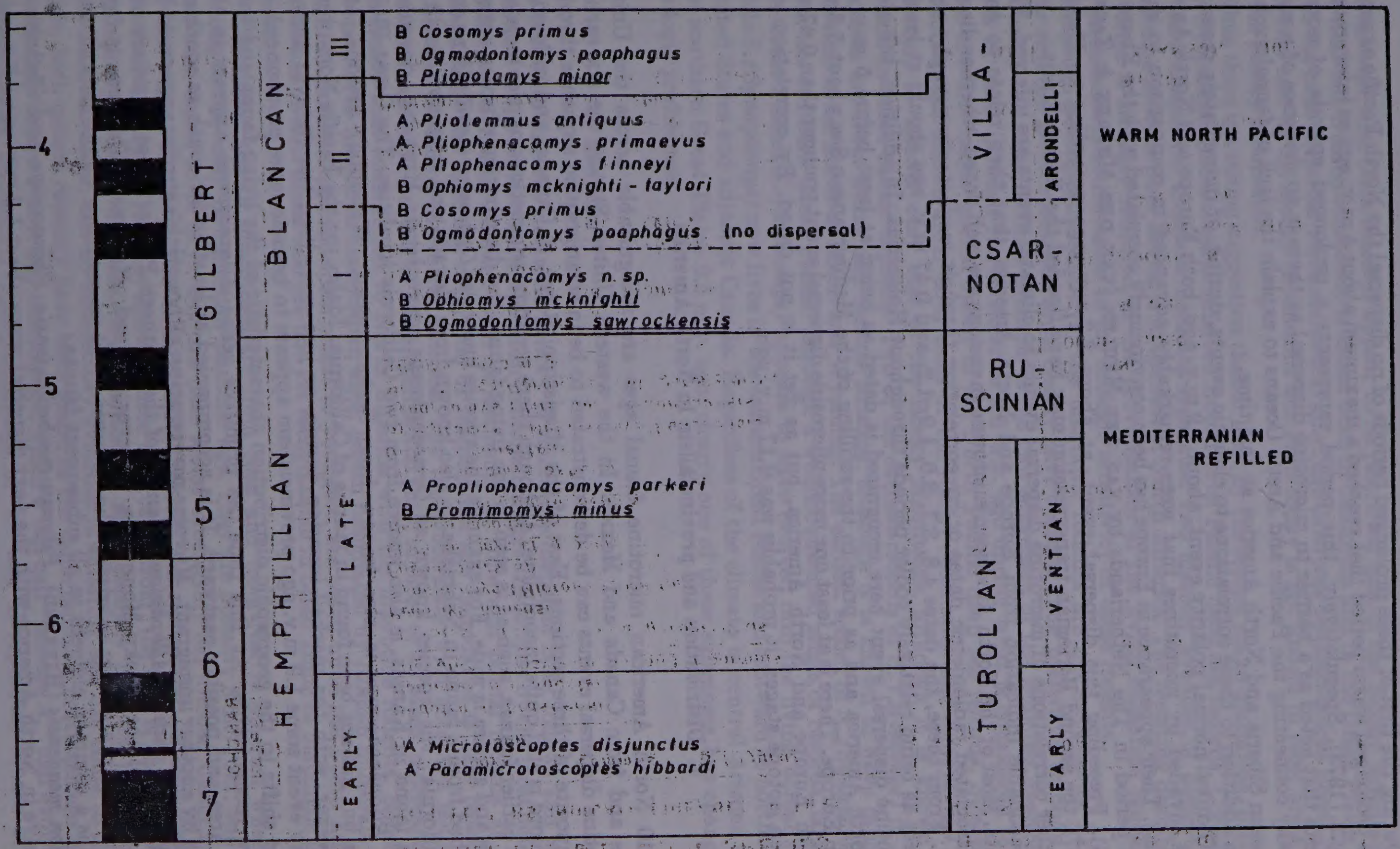

Table 1. Correlation of microtine dispersal events in North America to mammal ages and their subdivision based upon microtine faunal units and to other events. The bottom line of each box containing the characterizing microtine fauna is positioned at the time of the dispersal event.

During the first of these prolonged periods of no dispersal the North Pacific experienced a prolonged warm period that reached a maximum about 4 m.y. ago as interpreted by Ingle (1973). Speculatively, this period represents a prolonged episode of northern forests that acted as a barrier to microtine dispersal as there is no evidence of a marine seaway connecting the Pacific and Arctic Oceans to explain the lack of faunal exchange between Siberia and North America at this time.

In addition to these correlations to climatic events, during, or immediately preceding, the Olduvai normal polarity event, about 1.9 m.y. ago, both Europe and North America were invaded by microtines that were remarkably advanced in comparison to earlier faunas. Their appearance in Europe has been convincingly correlated with the Eburonian cold period in The Netherlands by van der Meulen (van der Meulen & Zagwijn 1974). Preceding this dispersal event, at about 2.2 m.y. ago according to Hopkins (1967), the second Beringian transgression may have flooded the Bering Strait.

Other correlations of microtine dispersal events to climatic events are inferred. There is reasonable indication from Europe and North America that they relate to cooler events. Most of the North American microtine invasions are well dated, whether directly by associated radiometric dates or by correlation through magnetostratigraphy or by both. From these, the dates 4.8, 3.7, 2.6, 1.9, 1.2, and 0.47 m.y. ago should at least be suspect as being relatively cooler periods throughout Holarctica. In addition, the oldest microtine dispersal event here recognized is dated as being at least before 5 m.y. ago in North America and as prior to the refilling of the Mediterranean Sea about 5.3 m.y. ago in Europe. There is at least one more microtine dispersal event younger than 0.47 m.y. in both Europe and North America, but as yet it is not dated. By correlation with oxygen isotope stages, it probably was 0.17 m.y. ago.

4. Distribution and provincialism in North America

The 10 North American microtine faunal ages are recognizable across the United States and from Canada and Mexico. In the western United States, the six earliest microtine dispersal events can be demonstrated to be in stratigraphic sequence through a composite of three sections. East of the Mississippi River, in Canada, and in Mexico, the record is still quite incomplete. Although there are some suggestions of provincialism in the earlier faunas, such as is seen in the living fauna, the distribution of some extinct species and genera is wide. For example the species known as *Ophiomys magilli* Hibbard, described from a fauna in Nebraska, is also known from Nevada and from two localities in California; the species known as *Ogmodontomys sawrockensis* Hibbard, described from a fauna in Kansas, is also known from two California localities. The Great Plains genus *Pliophenacomys* is also known from Saskatchewan, Wyoming, Arizona, and Sonora but has not been found in faunas of California, Idaho, or the Pacific Northwest.

However, with the marked invasion during, or just preceding, the Olduvai normal polarity event some 1.9 m.y. ago provincialism appears to become more pronounced, or at least shifts to the geographic distribution characteristic of the living fauna and thus is more recognizable. At this time the primitive genus *Allophaiomys* appears in the Plains area and possibly eastward. It is accompanied at least as far south as southern Canada by another immigrant, *Microtus paroperarius*, although this species appears to be missing in the earliest *Allophaiomys* faunas of the southern Plains. These forms are not known west of the Rocky Mountains, however; instead, *Microtus californicus* is first found in deposits closely overlying the Olduvai event in southern California and this species is a common element in all subsequent faunas.

Neodon meadensis (Hibbard), *Pitymys cumberlandensis*, *Phenacomys*, and *Clethrionomys* arrive in North America with the next dispersal wave about 1.2 m.y. ago; *Pitymys*, *Phenacomys*, and *Clethrionomys* appear to be restricted east of the Rocky Mountains at this time but *Neodon meadensis* is found both in California and in the Great Plains area. With the next dispersal wave about 0.47 m.y. ago *Microtus pennsylvanicus* floods North America east of the Rocky Mountains but even today is not known in most areas west of the Rocky Mountains.

Thus there is a strong suggestion that at least by the second major glaciation (probably the Nebraskan glaciation), as inferred from North Pacific deep sea records, Cordilleran ice and unsuitable montane habitats separated two distinct avenues of dispersal by microtine rodents from Beringia to the rest of North America. The resulting distribution of forms is strongly reflected in the provincialism of the living microtine fauna, and its persistence is attributable to the ecologic sensitivity of these rodents.

Although ecologically sensitive, the microtine rodents are not necessarily fixed in their ecologic preferences, and some clearly have changed their preference through time. Probably the most obvious example is the two subgenera of the lemming *Synaptomys*. Both of these invaded North America 2.6 m.y. ago during what is considered to have been the first major glacial epoch in the North Pacific deep sea records. *Synaptomys (Mictomys)* is known from both sides of the Rocky Mountains and *Synaptomys (Synaptomys)* is known only east of the Rocky Mountains, although it is known from Poland in much earlier deposits. Two of the earliest records of *S. (Mictomys)* in North America are from Texas and central Arizona, although it is known to have ranged at this time as far north as Idaho and Wyoming. The earliest record of *S. (Synaptomys)* is from the southern Great Plains. Through a welldocumented series of records, largely in the Great Plains, *S. (Mictomys)* appears to have evolved into the living boreal species while *S. (Synaptomys)* now lives in the eastern Great Plains and eastward to northeastern United States and adjacent Canada. Regardless of the climate in central Arizona and in the southern Great Plains 2.5 m.y. ago, clearly one of these subgenera has changed its ecologic preferences.

5. Biohistory

In broad outline the holarctic history of microtine dispersal is as follows and is summarized in the table. North American mammalian ages are defined by the most defensible definition of faunal content with adjustments in time and faunal records as herein recognized. The ultimate definition of mammalian age boundaries is here based upon microtine invasions of North America, but these correlate with accepted faunal differences that have proven to be defensible and that, in most or all cases, represent larger mammals that immigrated to North America with the microtine rodents. Subdivision of the North American mammalian ages, herein designated by Roman numerals within each mammalian age and from oldest to youngest, are based upon the North American microtine rodent fauna and are not yet recognizable in other kinds of mammals in most cases.

The oldest known microtines are from Asia and from North America where they belong to the early Hemphillian mammal age. They are possibly 8 m.y. old; one record has been dated at 10 m.y., but this date seems excessively old (Stroud Claim locality; EVERNDEN a. o. 1964). Two closely related genera are recognized: *Microtoscoptes* and *Paramicrotoscoptes*. It is not known where they came from; the first is known from Asia in equally ancient deposits. Hypothetically, *Microtoscoptes* is more primitive than *Paramicrotoscoptes*, but no satisfactory evidence of differing age has come to light. In fact, both genera recently have been found in the same fauna in northwestern Nevada.

Shortly before 5 m.y. ago this lineage, which I will call "lineage A," had evolved into the markedly different *Propliophenacomys* in the late Hemphillian faunas of North

America. At this same time a very primitive form of another microtine lineage, *Promimomys* of "lineage B", appeared in both Europe and North America, marking the first microtine dispersal event here recognized. This dispersal immediately followed the refilling of the Mediterranean Sea in Europe and it marks the beginning of the Ruscinian faunas. Only *Promimomys* is involved and the fact that it is far less specialized than contemporary North American representatives of "lineage A" suggests a separate origin out of the cricetid rodents that are ancestral to the microtines.

Around 4.8 m.y. ago two new forms of "lineage B" appear both in North America and in Europe to mark the beginning of Blancan I and Csarnotan faunas, respectively. In Europe these are referred to two subgenera of *Mimomys* and are so unmistakably more advanced than the prior representative of the lineage that a segment of evolutionary history is obviously lacking in both Europe and North America; records in northwestern Siberia record this evolution, however. In North America these two subgenera are usually placed in the genera *Ophiomys* and *Ogmodontomys*. In Europe, with these two forms of "lineage B", there known as *Cseria* and *Hintonia*, are found the first European representatives of "lineage A". These first "lineage A" immigrants in Europe are markedly more advanced than their contemporary immigrants belonging to "lineage B", but subsequent history suggests that they have about reached their peak in their rapid rate of evolution, and the one living form of Europe [*Dinaromys bogdanovi* (MARTINO)] shows little further advancement of specialization. "Lineage A" continued to evolve recognizably more advanced forms in North America.

There then followed the first prolonged period of no microtine dispersal that appears to correlate with a period of warmer North Pacific waters, as has been discussed. Forests possibly occupied Canadian North America and arctic Russia at this time, preventing dispersal out of Asian grasslands.

Between the invasion that marks the beginning of Blancan I and that marking the first Blancan III faunas, the prolonged period of no intercontinental microtine exchange is recorded by enough evolutionary change in endemic lineages to enable separation of Blancan I and Blancan II microtine faunas in North America. Similarly, the same prolonged period of no microtine dispersal events resulted in enough endemic evolutionary change in Europe to enable separation of Csarnotan faunas from the early (Arondelli "Phase") Villafranchian faunas. Ages thus defined upon endemic evolution have vague transitional boundaries, and the vagueness increases as a multiple of the number of lineages considered diagnostic. In addition they can have no relation to similar evolutionary stages in other continents not having faunal continuity, except by chance. In the definition of Blancan II, as distinct from Blancan I, three evolving microtine lineages are considered, and the approximate beginning of Blancan II faunas, at about 4.3 m.y.a., must be considered exactly that: approximate.

At about 3.7 m.y. ago the dispersal barrier appears to have been broken and, as has been mentioned, the first muskrat *(Pliopotamys)*, belonging to "lineage B", entered North America and the first lemming *(Synaptomys)*, belonging to "lineage C", entered western Europe along with a new genus of "lineage A" *(Villanyia)* and the *Elephas-Leptobos-Equus* fauna. These immigrants mark the beginning of Blancan III and the Rebielice "Phase" of the Villafranchian faunas. TEDFORD & GUSTAFSON (1977) have noted that a high proportion of the larger mammals that entered North America with the first muskrat suggest temperate forest environments; a good example is the panda that they discuss. The immigration of these forest elements would certainly be in agreement with the postulated preceding forest barrier and suggests only partial opening to microtine dispersal through which muskrats could pass but not the more grassland-oriented microtines.

As noted, the following 3.7- to 2.6-m.y.-ago period of no microtine dispersal into North America appears to correlate with the earlier Beringian transgression and the first opening of the Bering Strait (HOPKINS 1967). K/A dates in Iceland clearly indicate that during this period, at about 3 m.y.a., North Pacific marine mollusks dispersed to the North Atlantic (GLADENKOV 1976). As with the earlier long period lacking microtine immigration, this period from 3.7 to 2.6 m.y.a. was a span sufficient in duration that endemic evolution of the North American microtine fauna produced markedly distinct faunas. They are, therefore, subdivided into Blancan III and Blancan IV faunas on the basis of the evolution of two lineages and the presumed extinction of *Cosomys primus* less than 3 m.y.a. Their subdivision is obviously not a point in time but is gradational and poorly defined. They provide no basis for intercontinental correlation.

This period is culminated by the arrival of some lemmings *(Synaptomys)* in North America to mark the beginning of Blancan V. At this time SHACKLETON & OPDYKE (1977) indicate the first major glacial episode based upon deep sea oxygen isotope evidence. BOELLSTORFF (1978) has recently correlated the pre-Nebraskan till at Afton, Iowa, with events of this age. The oldest continental dates of this 2.6-m.y.-old dispersal event are 10 feet below the first beds recording the Matuyama reversed polarity epoch in Arizona (Tusker Fauna; E. H. LINDSAY, personal commun., 1978) and 2.5 m. K/A years in France (Roca Neyra of Villanyian age; SAVAGE & CURTIS 1970).

The immigration of the Asiatic subgenus *Synaptomys (Synaptomys)* only into areas east of the Cordillera suggests the beginning of dual avenues from Beringia into the rest of North America. But the marked provincialism indicating the establishment of a major immigration route along the east flank of the Cordillera does not appear until the Olduvai event about 1.9 m.y. ago.

Between the arrival of the first North American lemmings about 2.6 m.y. ago and the next dispersal wave about 1.9 m.y. ago the Bering Strait again formed. HOPKINS (1967) cites a date for the second Beringian transgression that falls within this span. North Pacific marine mollusks were, at this time, native to the Arctic and North Atlantic fauna, and any new marine dispersal, if such existed, has not been detected among the already "naturalized" North Pacific immigrants.

The renewal of Holarctic microtine dispersal during, or just before, the Olduvai normal polarity event about 1.9 m.y. ago, introducing Irvingtonian I genera, was the most dramatic immigration in the arvicolid history of both Europe and North America. This dispersal is dated in both Europe and North America as being at least as old as this paleomagnetic event and probably somewhat older. Abruptly the microtine faunas of North America and Europe assumed a "modern" appearance and consisted largely of species with rootless teeth, whereas rooted teeth were the common feature of earlier faunas. Genera referred to as *Microtus* and/or *Allophaiomys* are present in many faunas in North America. In addition, as has been discussed, the first clear-cut indication of the modern provincialism of microtine faunas within North America is evident and is presumably the result of two dispersal routes out of Beringia, a maritime route and an interior route—The Ice-Free Corridor—separated by an inhospitable Cordillera. With the new microtines came the mammoth and its associated large mammal fauna of the Irvingtonian age.

Many, but not all, of the "modern" microtines of the immigration of 1.9 m.y. ago actually were primitive and are now largely extinct in the areas where they are known as fossils. Many survive, however, in southern refuges as far south as Mexico, Guatemala, northern Burma, Tibet, and the Balkan and Iberian Peninsulas where *Microtus*, in a strict sense, is of limited variety or unknown. Such names as *Phaiomys* and *Neodon* are sometimes applied to them in the living fauna and almost without exception they survive in cooler mountain refuges. It appears that they were displaced southward by later waves of "even-more-modern" microtines. This displacement would have taken place during periods of southward-shifting climatic zones that permitted their escape but left them stranded in the mountain tops as the climate again warmed. It is also in these southern refuges that the living remnants of the oldest microtines belonging to "lineage A" still survive; such names as *Dinaromys*, *Hyperacrius*, *Ellobius*, and *Prometheomys* are applied to these in the Old World; none survive in North America.

After this first "modern-looking" microtine dispersal event 1.9 m.y. ago, the record in both Europe and in North America is one of immigration waves of even-more-modern-looking forms. At or shortly following 1.2 m.y. (Type S ash) *Pitymys* (in a strict sense), *Neodon*, *Phenacomys*, and *Clethrionomys* introduce Irvingtonian II faunas and become a part of the North American fauna; these are living genera although *Neodon* survives only in a small refuge in central Mexico (Repenning & Ferrusquia, in preparation). This dispersal event is difficult to recognize in Europa and, thus, is not well dated in Europe. Kent, Opdyke & Ewing (1971) have recorded a marked increase in ice-rafted detritus in the North Pacific beginning 1.2 m.y. ago and Shor & Poore (1979) find an abrupt increase in coarse erratics and the start of pronounced fluctuations in carbonate content at DSDP Site 410 in the North Atlantic at about this time.

Much less than 600,000 years ago, as dated in both Europe (post Matuyama) and North America (post Type O ash), the next microtine dispersal event introduced the Rancholabrean and living species *Microtus pennsylvanicus* and *M. montanus* to the North American fauna and *Arvicola* and *Lagurus* to the European Toringian fauna. The introduction of two species of *Microtus* would not seem so significant except that *M. pennsylvanicus* appears as a flood in almost every appropriate fossil locality east of the Rocky Mountains and is accompanied by larger mammals that characterize the Rancholabrean I mammalian age of North America. The correlative invasion of Europe marks the beginning of the early Toringian mammalian age which Kukla (1977) has correlated with the beginning of Oxygen Isotope Stage 12, about 475,000 years ago. Stage 12 is the most likely cold spell in the oxygen isotope chronology, to judge from its prominence, but the lack of better age control of the microtine dispersal event and the frequency of cold periods during the Brunhes normal polarity epoch make the correlation somewhat uncertain.

Although inadequate stratigraphic control may hide other microtine dispersal events, the present fossil record indicates only one additional invasion of Europe and North America; this event is undated but seems most probably to have taken place at the beginning of Oxygen Isotope Stage 6, roughly 175,000 years ago.

This last microtine dispersal event, possibly 175,000 years ago, introduced *Dicrostonyx*, *Lemmus*, and *Lagurus*, as well as many species of *Microtus* to the Rancholabrean II faunas of North America. Correlation to European invasions is weaker than with any other microtine dispersal event, largely because of the lack of means of dating faunas during this period of rapid climatic fluctuation, of no magnetic polarity reversal, and of inadequate radiometric methods. However, *Arvicola terrestris*, *Lagurus lagurus* and a number of species of *Microtus* first are known from this dispersal that marks late Toringian faunas of Europe. Tornewton Cave in England has a fossil record that appears to have begun with this invasion and that continued to the Holocene (Kowalski 1967). Its faunal succession records two cold spells prior to the Holocene; the younger includes more faunal horizons than the older and possibly includes other climatic fluctuations not recognized.

This dispersal event completes the modernization of the North American microtine fauna, a process that took 5 m.y. and that was marked by repeated invasions of more advanced microtine species and genera. Extinction of endemic forms was the rule with each new invasion and is helpful in the recognition of which of the 10 microtine ages thus defined is represented. But provincial evolution of endemic lineages is of more help, and, of course, new immigrants are the basis of the definition of most of these microtine ages.

Of the known microtine faunas of North America, no tribal lineage older than 3.7 m. y.

is represented in the modern fauna, only the muskrats survive from faunas older than 2.6 m.y. ago, and only the muskrats and the bog lemming *Synaptomys* survive from faunas older than 1.9 m.y. ago.

In summary, at 5.3, at 4.8, about 4.3, at 3.7, about 2.9, at 2.6, at 1.9, at 1.2, at 0.47, and possibly at 0.17 m.y. ago the North American microtine fauna changed into distinctly different faunas. The two faunas that began about 4.3 and 2.9 m.y. ago resulted from endemic evolution; these appear to correlate with prolonged periods of warm North Pacific water temperatures. The second of these is believed to have been in existence during the first opening of the Bering Strait and approximates in time the first arrival of Pacific marine mollusks in Iceland. The well-dated invasions at 2.6 and 1.9 m.y. correspond to early major glaciations in the northern hemisphere and are separated by the second Beringian transgression; the first appears to correlate with a pre-Nebraskan continental glacial advance, and the distribution of microtines during the second strongly suggests the presence of a Cordilleran ice field.

It is to be noted that the invasions as dated in continental deposits correlate with the early part of the ^{18}O increasing-percentage trend leading to the maximum that is inferred as indicating significant land ice; they do not correlate with the maximum ^{18}O percentage. In published sources, oxygen isotope data around 1.2 m.y. ago appear weak, but this microtine invasion correlates well with the evidence of ice-rafted detritus in the North Pacific and is dated by the Type S ash of the Plains area (IZETT 1977). Dating of the 0.47 m.y. invasion in North America is only considerably less than 0.6 m.y., and 0.47 m.y. was selected to coincide with the ^{18}O data of glacial maxima; KUKLA (1977) has already correlated this microtine invasion in Europe, the beginning of the Toringian mammalian age, with this date. The last microtine invasion of North America is not dated but probably correlates with ^{18}O Stage 6 at about 0.17 m.y. ago.

6. Cape Deceit, Alaska

One North American fossil fauna that does not conform to these microtine stages is the Cape Deceit Fauna of western Alaska described by GUTHRIE & MATTHEWS (1971). Except for this fauna, the lemmings *Lemmus* and *Dicrostonyx* are unknown in North America before Rancholabrean II faunas, marked by the last recognized invasion of which they are a part. The history of *Dicrostonyx* is becoming well known in both Europe and Asia, and the form, *Predicrostonyx*, from Cape Deceit cannot be as young as 175,000 years. More modern forms are known 1.8 m.y. ago in Europe, and *Predicrostonyx* is known in Siberia (VANGENGEIM 1977) from faunas here correlated with Blancan V and Irvingtonian I faunas of North America: possibly as old as 2.5 m.y.

In addition, the Cape Deceit Fauna contains a microtine that GUTHRIE and MATTHEWS correctly describe as very primitive and name *Microtus deceitensis*. At least some specimens assigned to this species belong in the Asiatic genus *Lasiopodomys*, although they are more primitive than the living species and most resemble *Lasiopodomys prebrandti* (ERBAEVA 1976) known from Siberian faunas correlated with Blancan V faunas. *Lasiopodomys* is considered a subgenus of *Microtus* by most neontologists but has a long and separate history according to studies in Asia by ERBAEVA (1976). The chronology of this history is not clear as yet, but *Lasiopodomys deceitensis* is similar to the most primitive form, which is only slightly advanced over a *Mimomys* tooth pattern. In addition to being distinguishable on tooth morphology, *Lasiopodomys* is sharply distinct from *Microtus* in behavior and vocal abilities; although smaller, it lives the life and makes the sound of a prairie dog. It is exclusively Asiatic, except for the Cape Deceit fauna.

Pliomys deeringensis from the Cape Deceit Fauna does not neatly fit into this genus but could belong here; the hesitation to include it stems partly from the poorly known history and diversity of the Asian microtines. If the generic assignment is correct, it is the only representative of this genus to enter North America. The known history of the genus is European, although fossil and living microtine faunas indicate that it also was native to Asia.

Most obviously, the Cape Deceit Fauna does not fit into North American microtine faunal history. It is a Siberian fauna found in Beringia on the wrong side of Bering Strait. Lack of similarity to other North American faunas indicates that it lived in Alaska during a period when there was no microtine dispersal event in progress which leads to the conclusion that Canadian and southern Alaskan forests, not the Bering Strait, were the barrier preventing microtine dispersal at this time. This conclusion does not indicate an age older than the Bering Strait, of course, but preliminary evaluation of the microtine fauna on the basis of Siberian records strongly suggests a pre-Pleistocene age correlative to North American Blancan V faunas and approximate contemporaneity with the second Beringian transgression of Hopkins (1967).

Acknowledgment

This summary of the history of microtine dispersal between Siberia and North America is based upon a study of the holarctic correlation of microtine rodents in preparation by the author and his associate, Oldřich Fejfar of the Geological Survey, Prague, Czechoslovakia. To Dr. Fejfar considerable thanks are expressed for his assistance in my understanding of the microtine biostratigraphy of Europe (see Fejfar 1976) and for encouraging me to renew my interest in microtine rodents, which has been dormant since 1967. Considerable revision in the classification of North American fossil microtine rodents and a great number of unpublished fossil faunas are to be incorporated in this joint study and are not discussed in the present short paper. Preliminary discussions of this work are to be found in Repenning & Fejfar (1977 and 1978); these are outdated to some degree.

Summary

The microtine rodents, because of their rapid rate of evolution in recent geologic time, their arctic to temperate preferences, and their rapid rate of dispersal in appropriate environments, provide the most precise record of faunal movement between Siberia and North America. This record has been calibrated by radiometric dates, the paleomagnetic polarity scale, oceanic climatic indicators, and the similar history of microtine invasions from Siberia into Europe. The development of provincialism in the North American fossil microtine fauna clearly documents the effective beginning of the Ice-Free Corridor east of the Cordilleran ice field. Between microtine dispersal events, Beringian Alaska had a Siberian fossil fauna bearing no relation to that of North America.

Zusammenfassung

Die microtinen Rodentier liefern wegen ihrer sehr hohen Evolutionsrate in jüngster geologischer Vergangenheit, ihrer bevorzugten Verbreitung im arktischen bis gemäßigten Bereich und ihrer sehr raschen Ausbreitung in den ihnen zusagenden Lebensräumen die genauesten Belege für den Faunenaustausch zwischen Sibirien und Nordamerika. Diese Belege wurden mit Hilfe radiometrischer Daten, paläomagnetischer Angaben, ozeanischer Klimaindikatoren und der sehr ähnlichen Geschichte der Microtinen-Invasionen von Sibirien nach Europa geeicht. Die Entstehung des Provinzialismus in nordamerikanischen fossilen Microtinenfaunen dokumentiert klar das Wirksamwerden eines eisfreien Korridors, der östlich vom Inlandeis der Kordilleren lag.

Die Zeiträume zwischen den Ausbreitungswellen der Microtinen sind im amerikanischen Teil von Beringia (Alaska) durch eine fossile Fauna sibirischer Herkunft gekennzeichnet, die keine Beziehungen zu derjenigen von Nordmerika aufweist.

Резюме

Из-за высокой их эволюционной скорости в ближайшем геологическом прошлом, их предпочтительного распространения в арктической и умеренной зонах и их способности к быстрому расселению в подходящих для них пространствах микротидные грызуны дают наиболее точные материалы для суждения об обмене фаун между Сибирью и Северной Америкой. Эти данные подкреплены радиометрическими и палеомагнетическими датировками, океаническими индикаторами климата, а также весьма сходной историей инвазий половёк из Сибири в Европу. Возникновение ,,провинсиализма'' в североамериканских ископаемых фаунах микротид ясно свидетельствует о наличии свободного ото льда коридора, который был расположен восточнее континентального ледяного щита на Кордильерах. Временные промежутки между волнами расселения микротид в американской части берингийской суши обозначены ископаемой фауной сибирского происхождения, которая не обнаруживает каких-либо связей с североамериканской.

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